

## Fossil Vesicomyid Bivalves from the North Pacific Region

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*Abstract.* A review of the fossil record of vesicomyid bivalves from the North Pacific region (Hokkaido, Japan; Alaska and Washington, USA) allows the clarification of the status of several species based on new data and observations, and four new species are recognized. Detailed examination of the hinge of *Hubertschenckia ezoensis* shows that *Hubertschenckia* is a valid monotypic genus closely related to *Archivesica* and *Calyplogena*. Specimens of ‘*Calyplogena*’ *chinookensis* from its late Eocene type locality at Bear River have a hinge structure that clearly places this species in *Adulomya*; silicified ‘*C.*’ *chinookensis* specimens described earlier from the late Oligocene have a very different hinge structure and are assigned to the new species *Archivesica knapptonensis*. The hinge dentition of all three Cretaceous vesicomyids proposed so far is unknown and their validity is doubtful. With *Hubertschenckia ezoensis*, *Adulomya chinookensis*, and *Archivesica* cf. *tshudi*, three genera of large vesicomyids appear more or less simultaneously at methane seeps in the late Eocene. Of Oligocene age are the new species *Archivesica georgemoorei* from Alaska, which is shorter and more oval than other known *Archivesica* species, and a possible *Phiocardia?* sp. from cold seeps in Washington. From the early Miocene of Washington *Isorropodon frankfortensis* is described and represents the first certain record of this genus from outside the Atlantic realm. The new middle Miocene *Adulomya hokkaidoensis* is so far only known from a whale-fall community in Hokkaido and may have been endemic to this type of habitat. The timing of the occurrences of these taxa shows no correlation to the evolution of whales in this area, shedding further doubt on the ‘whale stepping-stone’ hypothesis for the origin of vesicomyids.

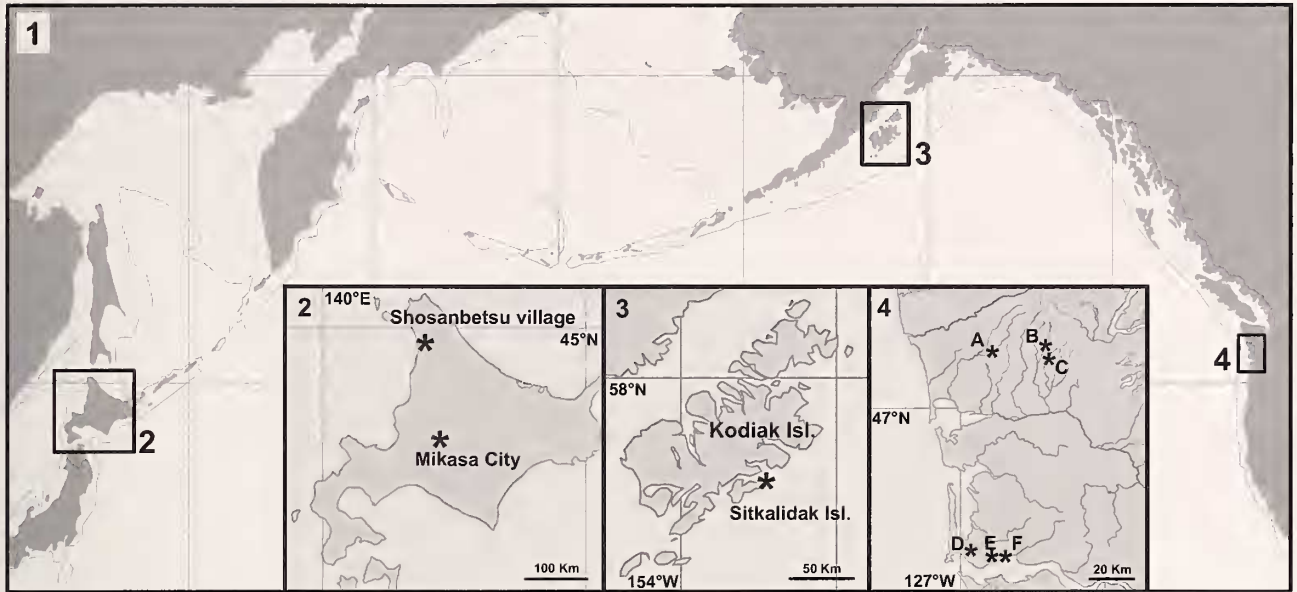
### INTRODUCTION

Fossil vesicomyid bivalves in the North Pacific region, especially in Japan, have been described for more than a century (Yokoyama, 1890; Majima et al., 2005; Amano & Kanno, 2005). However, vesicomyids received little scientific attention until the discovery of the ‘Giant White Clam’ *Calyplogena magnifica* at hydrothermal vents on the Galapagos Ridge in the late 1970s (Boss & Turner, 1980). Since then they have been found in many chemosynthesis-based ecosystems at hydrothermal vents, hydrocarbon seeps, and whale carcasses throughout the world’s oceans (Van Dover, 2000; Van Dover et al., 2002; Kojima, 2004). These discoveries led paleontologists to take a new look at vesicomyid occurrences, and many of these sites have since been identified as fossil hydrocarbon-seep deposits.

The occurrence of vesicomyids at decaying whale carcasses in the deep-sea (whale-falls) led to the formulation of the ‘stepping stone’ hypothesis. This hypothesis suggested that whale-falls provide dispersal stepping stones for vent and seep taxa, and that therefore the rise of whales in the Eocene suddenly (geologically speaking) extended the dispersal capabilities of vent and seep taxa, resulting in a significant radiation among these animals (Baco et al., 1999; Smith

& Baco, 2003). This hypothesis was based on the rough correlation between the evolutionary age of vesicomyids estimated from molecular clocks and the first appearance of whales in the Eocene (Baco et al., 1999; Smith & Baco, 2003). Squires et al. (1991) and Goedert et al. (1995) however, had already pointed out that in the North Pacific, seep taxa such as vesicomyid bivalves were already very widely distributed before the earliest known appearance (latest Eocene) of whales in the region. The stepping-stone hypothesis was challenged by Little & Vrijenhoek (2003) who called attention to the discrepancy between the molecular age estimates for vesicomyids [21.5–43.8 Ma according to Peek et al. (1997)] and the oldest fossil vesicomyids from the Early Cretaceous (upper Albian, 106 Ma) in northern Japan (cf. Kanie et al., 1993; Kanie & Sakai, 1997). It was also challenged by Kiel & Goedert (2006) who showed that vesicomyids and other taxa characteristic of modern whale-falls were absent from Eocene and Oligocene whale-falls and only appeared in Miocene examples.

However, a thorough analysis of the fossil history of the Vesicomyidae and its potential correlation with the radiation of whales has so far been hampered by the inconsistent use of generic names and concepts within



Figures 1–4. Locality maps of fossil specimens. Figure 1. Map showing the general location of the fossil sites described herein. Figure 2. Hokkaido, Japan, asterisks indicate the two fossil sites. Figure 3. Kodiak Island, Alaska, asterisk indicates the fossil locality on nearby Sitkalidak Island. Figure 4. Localities in western Washington State, USA, A=Humpulips River sites, B=Canyon River site, C=Satsop River site (LACMIP loc. 17747), D=Bear River site (LACMIP loc. 5802), E=Knappton (LACMIP loc. 5843), F=Frankfort (USGS loc. M2790).

this family (see Krylova & Sahling, 2006 for a review), which partly results from incomplete knowledge of several of the type species. Important progress was made recently by Cosel & Salas (2001) who revised the genera *Vesicomya*, *Waisiuconcha*, *Isorropodon*, and *Callogonia*, by Krylova & Sahling (2006) who redefined *Calyptogena* and revised its Recent species, and by Kiel (2007) who clarified the status of *Pleurophopsis*.

The aim of this paper is to revise some of the fossil vesicomomyids from the North Pacific region (Figure 1) based on newly collected material. We describe four new species from Japan, Alaska, and Washington, and provide revised generic diagnoses for *Adulomya* Kuroda, 1931, *Archivesica* Dall, 1908, and *Hubertschenckia* Takeda, 1953. Finally, we discuss the evolutionary implications of our findings.

#### MATERIAL, STRATIGRAPHY, AND OCCURRENCES

All Japanese specimens described here are housed in the Joetsu University of Education (JUE). Material from Washington State will be housed in the Smithsonian Natural History Museum (USNM) and the Natural History Museum of Los Angeles County (LACMIP), the specimens from Alaska will be housed in the Museum of Paleontology, University of California, Berkeley (UCMP). Locality numbers of the United States Geological Survey (USGS) and the

California State University, Northridge (CSUN) are also used herein.

#### Japan, Hokkaido

**Poronai Formation:** The Poronai Formation is a 1100 m-thick sequence of deep-water mud- and siltstone of late Eocene age, cropping out in central Hokkaido (Kaiho, 1983, 1984). Seventeen specimens of *Hubertschenckia ezoensis* were collected from a cold-seep deposit at a high cliff along the Ikushunbetsu River, 200 m to the west of Yayoi Town in Mikasa City (Figure 2; see Amano & Jenkins, 2007 for more details). Here, a calcareous concretion approximately 2 m in diameter occurs in dark gray mudstone of the Poronai Formation (B Zone of Teshima, 1955). The *Hubertschenckia* specimens occur mostly within this concretion but also directly adjacent to it. Almost all specimens are articulated, but also a few disarticulated valves were collected. The Yayoi fauna in the surrounding mudstone consists of the protobranch bivalves *Acila (Trumacila) picturata* (Yokoyama), *Malletia poronaiica* (Yokoyama), *Portlandia (Portlandella) watasei* (Kanehara), the thyasirid bivalve *Conchocele bisecta* (Conrad), the carditid bivalve *Cyclocardia tokudai* (Takeda) and the caenogastropod *Orectospira wadana* (Yokoyama). The faunal composition of the molluscan assemblage is similar to the lower sublittoral to upper bathyal *Malletia poronaiica*-

*Cyclocardia tokudai* assemblage of Suzuki (2000) from the lower part of the Poronai Formation. In addition, Kaiho (1984) used benthic foraminifers to infer a maximum depth of 350 m for deposition of the Poronai Formation.

**Chikubetsu Formation:** The Chikubetsu Formation is of middle Miocene age and subdivided into the lower sandstones (210 m) and the upper siltstones (230 m) (Noda, 1992). When Amano & Little (2005) recorded a Miocene whale-fall community from the uppermost part of the Chikubetsu Formation, they illustrated two specimens and the hinge of a left valve of *Calyptogena* sp. These were collected from a large roadside cliff along the Setakinai River, 5.5 km upstream from Shosanbetsu Village in northern Hokkaido (Figure 2; see Amano & Little, 2005 for more details). Subsequently, one right valve with a distinct pallial line and a specimen with the hinge of the right valve preserved were collected from the same locality. All specimens occurred in a bone-bearing concretion in siltstone. As inferred by Amano & Little (2005), this community might have lived below the middle-bathyal zone, based on benthic foraminifers (cf. Maiya et al., 1982).

#### USA, Alaska

**Sitkalidak Formation:** This formation is of Eocene to Oligocene age and occurs in a series of patches at the southeastern tips of points on Kodiak, Sitkalidak, and Sitkinak Islands. It is a rather uniform, about 3000 m-thick sequence of graded sandstone and siltstone beds, with a few conglomerate beds (Moore, 1969). The new species *Archivesica georgemoorei* was found near the top of the Sitkalidak Formation in the type area on the north shore near the east end of Sitkalidak Island (Figure 3), where it co-occurred with the thalassinid shrimp *Callianassa* aff. *porterensis* (cf. Moore, 1969). The dating of this site is somewhat uncertain, because it is solely based on the lithological similarities between the Sitkalidak Formation, the Burls Creek member of the Katalla Formation (Alaska), and the Blakeley Formation (Oregon) (F. S. MacNeil, written communication to G. W. Moore, 13 Aug. 1963). The fossil site is most likely a hydrocarbon-seep deposit (Goedert et al., 2003).

#### USA, Washington State

**Astoria Formation:** This formation crops out on the north shore (Washington) and south shore (Oregon) of the Columbia River. In Washington, rocks referred to as Astoria Formation in Pacific and Wahkiakum counties are 750 to 1000 m in thickness, and consist of thick-bedded, coarse-grained grayish-brown marine sandstone and soft, dark-gray siltstone (Moore, 1963; Wolfe & McKee, 1972; Wells, 1989). The new species

*Isorropodon frankfortensis* was recovered by acid etching from two small blocks of cold-seep carbonate found as float on beach terraces near the abandoned settlement of Frankfort (Figure 4F). The type locality of *Isorropodon frankfortensis* is equivalent to locality M-25 of Wolfe & McKee (1972) and USGS loc. M2790. Wolfe & McKee (1972) noted that the sediments in this area were deposited at a depth between 16 and 650 m.

**Humptulips Formation:** This formation crops out on the southwestern slope of the Olympic Mountains (Figure 4A), is approximately 1000 m thick (Rau, 1986), and is of late middle Eocene age (Prothero et al., 2001). It consists of siltstone and mudstone, and beds of structureless sandy siltstone, deposited at depths estimated to have been between 1500 and 2000 m (Rau, 1986). Several seep carbonates have been reported from this formation, containing, among other fossils, *Calyptogena chinookensis* and *Vesicomya* sp. (Squires & Goedert, 1991, 1996; Goedert & Kaler, 1996). The latter species is here described as *Archivesica* cf. *tshudi* (Olsson, 1931). The new material was found in a small seep limestone block on a gravel bar in the East Fork of the Humptulips River, approximately 400 m west and 600 m north of the southeast corner of Sec. 6, T20N, R9W, Grays Harbor County, Washington. The source of this material is likely the high cliff just upstream and on the south side of the river at the sharp bend, either allochthonous cold-seep limestone, or an *in situ* seep deposit. Additional specimens are from seep carbonate at CSUN loc. 1583.

**Lincoln Creek Formation:** This formation is an approximately 3000 m thick sequence of deep-water mud- and siltstones of late Eocene to early Miocene age, that crops out in western Washington State, between the southern slopes of the Olympic Mountains and the Columbia River. *Archivesica knapptonensis* n. sp. is from two late Oligocene seep-carbonate outcrops of the Lincoln Creek Formation. Blocks of seep carbonate were collected on tidal terraces near Knapp-ton on the north shore of the Columbia River at LACMIP loc. 5843 (Figure 4E). The age of this locality was considered early Miocene by Moore (1984) and late Oligocene by Goedert & Squires (1993). The vertebrate assemblage of this locality indicates that late Oligocene is the more probable age of these sediments (Barnes & Goedert, 2001; and J. L. Goedert, personal communication 2005). The mollusk fauna indicates a depositional depth of 100 to 350 m, whereas benthic foraminifers indicate 300 to 1000 m depth (Moore, 1984). At another site (Figure 4B, referred to as 'Canyon River site' herein) occur carbonate 'blebs' with small mollusks and a very large bivalve (*Cryptolucina?*) on a low bench on the east side of the Canyon River, approximately 40 m north and 260 m east of the

southwest corner of Sec. 25, R7W, T21N, Grays Harbor County. This site is of Oligocene age. A locality on the Satsop River (Figure 4C; LACMIP loc. 17747b; Oligocene) yielded a specimen of *Pliocardia?* sp. with a drill hole. Seep-related mollusks were described from two other carbonate blocks from that site by Kiel (2006), who also provided more details about the locality.

**Siltstone of Cliff Point:** Deep-water siltstones crop out on the north shore of the Columbia River, to the west of the Lincoln Creek Formation. Wells (1989) stated that this unit may be correlative with the 'Siltstone of Unit B' of Wolfe & McKee (1972). The 'Siltstone of Unit B' was deposited at depths between 300 and 1,000 m (Wolfe & McKee, 1972). A large seep carbonate in this formation at LACMIP loc. 5802 (Figure 4D) is the type locality of '*Calyptogena chinookensis*' Squires & Goedert, 1991. The hinge dentition of two specimens from this site is described to clarify its systematic position.

## SYSTEMATIC DESCRIPTIONS

### Family VESICOMYIDAE Dall & Simpson, 1901

**Remarks:** The Vesicomylidae are used here in the traditional sense. Based on anatomical and conchological observations on Recent North Atlantic species of *Kelliella* Sars, 1870 and *Vesicomya* Dall, 1886, Allen (2001) suggested that the Vesicomylidae should be synonymized with Kelliellidae. However, Cosel & Salas (2001) noted that Allen (2001) had misidentified some of his *Kelliella* species and pointed out distinctive differences between *Kelliella* and *Vesicomya*; hence, retaining the name Vesicomylidae.

The various genera related to *Calyptogena* Dall, 1891 are currently used very differently in the literature. On one end of the spectrum, Coan et al. (2000) treated *Calyptogena* as a subgenus of *Vesicomya*; *Akebiconcha*, Kuroda, 1943, *Archivesica* Dall, 1908, *Ectenagena* Woodring, 1938, and *Phreagena* Woodring, 1938 were considered synonyms of *Calyptogena*. On the other end of the spectrum, Keen (1969) considered all hitherto proposed names valid, except for *Adulomya* Kuroda, 1931, which was erroneously placed in the Solemyidae. Based on a combination of conchological and molecular data, Okutani et al. (2000) and Sasaki et al. (2005) recognized three subgenera of *Calyptogena*: *Calyptogena* s.s., *Archivesica*, and *Ectenagena*. This classification scheme is largely followed here, with the modifications that *Ectenagena* is shown here to be a junior synonym of *Adulomya*. The latter and *Archivesica* are considered herein to be independent genera.

We provide translated and emended generic diagnoses for these genera, based on our own observa-

tions. Figure 5 shows the main hinge features that characterize these genera. Table 1 gives an overview of their synonymies. We provide a list of the fossil species that we consider to belong to each of the genera; however, a full revision of the Recent species is beyond the scope of this study.

### Genus *Hubertschenckia* Takeda, 1953

*Hubertschenckia* Takeda, 1953:85.

**Type species:** *Tapes ezoensis* Yokoyama, 1890 (by monotypy); Poronai Formation, upper Eocene, Hokkaido, Japan.

**Taxonomic history:** *Hubertschenckia ezoensis* was initially described by Yokoyama (1890) from "Cretaceous" deposits (=Eocene Poronai Formation) around Poronai on Hokkaido, and placed in the venerid genus *Tapes* Mühlfeld, 1811. Minato & Uozumi (1951) were the first who illustrated the hinge dentition of a left valve and noticed that this hinge resembles that of *Akebiconcha* Kuroda, 1943. Following the advice given to them by Dr. Tokubei Kuroda, they placed the species in the Veneridae and suggested that it may belong to a new genus.

When Takeda (1953) eventually proposed *Hubertschenckia* based on *Tapes ezoensis*, he placed it in the Veneridae and indicated a late Oligocene age for the Poronai Formation. He re-illustrated the figure of the left valve hinge provided by Minato & Uozumi (1951) and described the hinge structure as follows: 1) presence of laterals, 2) diminishing of anterior cardinal, 3) bifid middle cardinal in the right valve, 4) fusion of anterior lateral with cardinal tooth in the left valve. However, his description of the hinge dentition of the right valve was taken mainly from notes provided to him by Dr. Takumi Nagao, and he erroneously described the anterior cardinal teeth (2a, 3a) as anterior lateral teeth. Moreover, the bifid tooth in the right valve is the posterior cardinal one (3b), not the middle one. Oyama et al. (1960) also placed *Hubertschenckia* in the Veneridae. Keen (1969) illustrated the same specimen as Minato & Uozumi (1951) and Takeda (1953), followed Takeda's description, and placed *Hubertschenckia* in the Vesicomylidae. Subsequent workers have followed this placement (Kanno, 1971; Habe, 1977; Boss & Turner, 1980; Krylova & Sahling, 2006). Also Keen (1969) gave the stratigraphic age as Oligocene, following Takeda (1953). Then, Kaiho (1983, 1984) assigned the age of Poronai Formation to the late Eocene. Kanno & Teshima (1994) described *Hubertschenckia ezoensis* again and mentioned the following characteristics: 1) thin anterior cardinal tooth of left valve along dorsal margin, connecting with the middle tooth under the umbo, 2) existence of a subumbonal pit in juvenile specimens, but not developed in

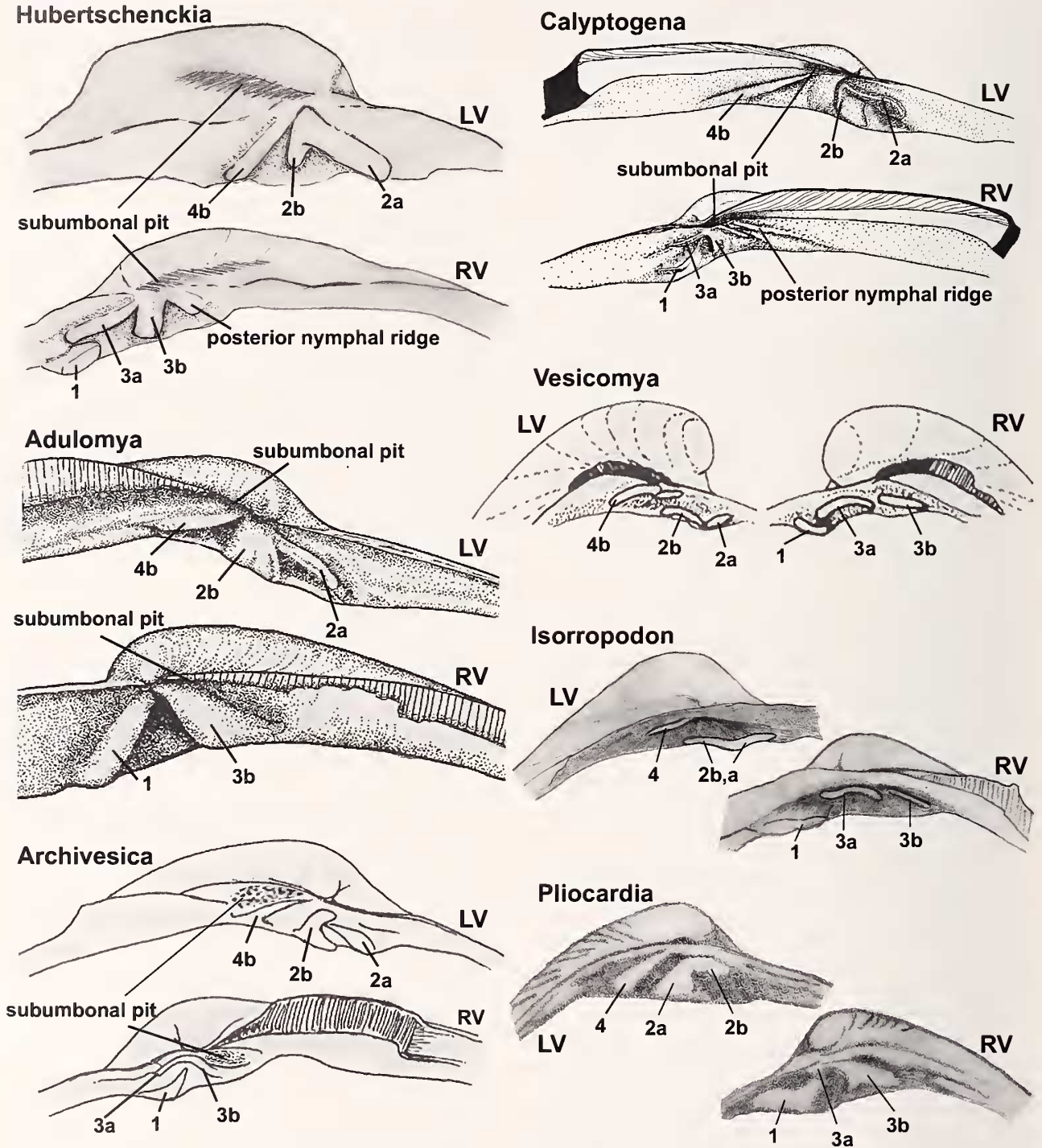


Figure 5. Terminology of the main hinge characters used in the text; not to scale. Sources: *Hubertschenckia* drawn from the specimens figured herein on Figures 6–7; *Adulomya* from Boss & Turner (1980:fig. 10E, of the holotype of *Adulomya elongata*); *Archivesica* from Okutani et al. (2000:fig. 12, which is based on specimen L99264A1-54 of *Archivesica gigas* provided by the Monterey Bay Aquarium Research Institute); *Calyptogena* from Krylova & Sahling (2006:fig. 2, source not specified); *Vesicomya* from Cosel & Salas (2001:figs. 76–77, based on a specimen of *Vesicomya adamsi* collected off Namibia); *Isorropodon* redrawn from specimens of *Isorropodon perplexum* figured by Cosel & Salas (2001:figs. 44 and 47); *Pliocardia* redrawn from Woodring's (1925, pl. 20, figs. 3 and 5) figures of *Pliocardia bowdeniana*.

Table 1  
Type species and synonymies of the genera used herein.

Genus	Type species	Synonyms
<i>Adulonia</i> Kuroda, 1931:27.	<i>Adulonitya uehimuraensis</i> Kuroda, 1931	<i>Ectenagena</i> Woodring, 1938:51. ? <i>Pleurophopsis</i> Van Winkle, 1919:23.
<i>Archivesica</i> Dall, 1908:418.	<i>Callocardia gigas</i> Dall, 1896	<i>Akebiconcha</i> Kuroda, 1943:17. <i>Phreagena</i> Woodring, 1938:50.
<i>Hubertschenckia</i> Takeda, 1953:85.	<i>Tapes ezoensis</i> Yokoyama, 1890	
<i>Isorropodon</i> Sturany, 1896:17.	<i>Isorropodon perplexum</i> Sturany, 1896	
<i>Pliocardia</i> Woodring, 1925:147.	<i>Anomalocardia bowdeniana</i> Woodring, 1903	

adults, 3) existence of a pallial sinus throughout the entire ontogeny, suggesting an infaunal mode of life. This characterization agrees with our observations, except that the subumbonal pit can in fact also be observed in adult specimens.

**Remarks:** *Archivesica* is most closely related to *Hubertschenckia* in having a bifid posterior cardinal tooth (3b) in the right valve, a subumbonal pit, and a shallow pallial sinus. However, the hinge dentition of *Hubertschenckia* is more primitive than in *Archivesica* from the viewpoint of evolutionary change of the heterodont hinge (Cox et al., 1969). *Hubertschenckia* has a long anterior cardinal tooth (3a), a long central tooth (1) along basal margin of hinge, and a stout vertical posterior one (3b) in the right valve. *Hubertschenckia* shares with *Calypptogena* the posterior nymphal ridge and the posterior cardinal (3b) that points in an anteroventral direction.

*Hubertschenckia ezoensis* (Yokoyama, 1890)

(Figures 6–12)

*Tapes ezoensis* Yokoyama, 1890:197, pl. 25, figs. 6–8.

*Tapes* (new gen.?) *ezoensis* Yokoyama. Minato & Uozumi, 1951:150, pl. 13, figs. 108a–c.

*Hubertschenckia ezoensis* (Yokoyama). Takeda, 1953:85, pl.13, fig. 5; Oyama et al., 1960:188–189, pl. 58, figs. 2a–d.

non *Meretrix* (*Macrocallista*) *ezoensis* (Yokoyama). Yokoyama, 1928:77, pl. 8, fig. 1.

non *Hubertschenckia ezoensis* (Yokoyama). Honda, 1989:79, figs. 13, 14.

**Material:** Seventeen specimens from the Poronai Formation at Yayoi, Mikasa City, Hokkaido. For measurements of shell length, height and thickness see Table 2.

**Type locality:** Poronai, Mikasa City, Hokkaido.

**Type material:** Yokoyama (1890) did not designate a holotype. He mentioned that 'several' specimens were available, figured three of them, and made no

indications as to their repository. At the time of writing his report, Matajiro Yokoyama was based in Munich, Germany, and the specimens may have been deposited in the Bavarian State Collection. However, they could not be located there (A. Nützel, personal communication 2007), and may either have never been deposited there, or were destroyed during World War II. Takeda (1953, p. 86) indicated that the holotype is 'preserved in Tokyo University,' where it could not be located (T. Sasaki, personal communication 2007), and that a syntype from the collection of Dr. Satoru Uozumi is deposited as UH. Reg. No. 11181 at Hokkaido University in Sapporo. Because the holotype could neither be located in Munich nor in Tokyo, it is considered lost and we designate the specimen UH. Reg. No. 11181 as neotype.

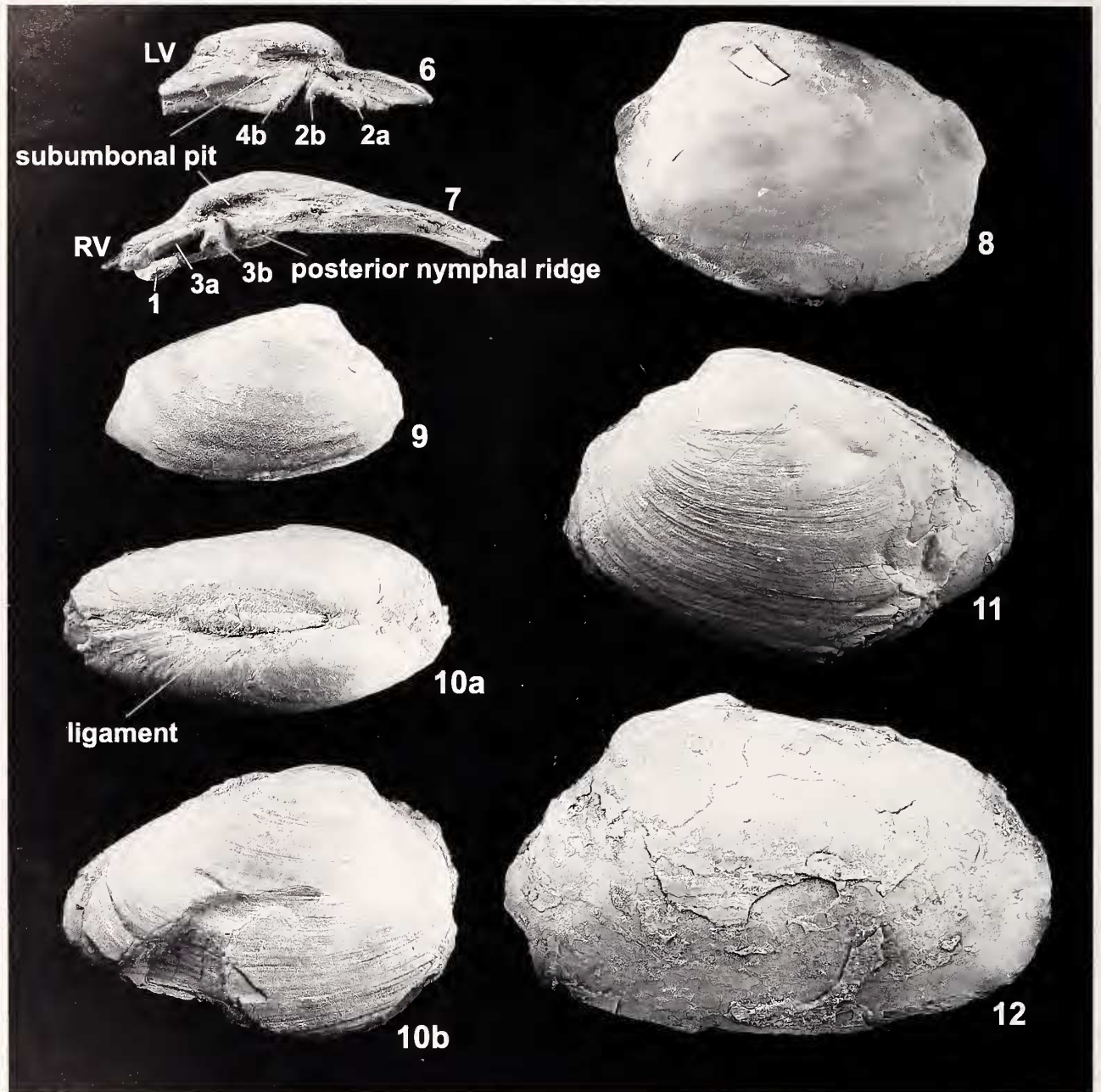
**Original description (translated from the German by SK):**

"We have several specimens, but with only partly preserved shell. Shell thick, moderately convex, elongate elliptical, strongly inequivalved; posterior side approximately 2 ½ times as long as anterior side. Anterior and posterior margins rounded; ventral margin only slightly convex, almost parallel to hinge. Beaks small, pointed, curved, almost touching each other. The surface shows only irregular, concentric growth lines. The anterior muscle attachment scar is pear-shaped, the posterior one rounded. Sinus finger-

Table 2

Measurements of *Hubertschenckia ezoensis* specimens.

No. of specimens	Length (mm)	Height (mm)	Thickness (mm)
JUE no. 15837-1	74.6	43.7	29.3
JUE no. 15837-2	73.0	41.1	28.4
JUE no. 15837-3	72.8	40.0	32.6
JUE no. 15837-4	65.3	39.0	29.0
JUE no. 15837-5	56.7	29.1	24.1
JUE no. 15837-6	50.9	32.1	22.4
JUE no. 15837-7	35.4	24.5	17.1
JUE no. 15837-8	27.2	17.4	10.2
JUE no. 15837-9	17.6	10.0	8.1



Figures 6–12. *Hubertschenkia ezoensis* (Yokoyama). Figure 6. Left-valve hinge, hinge length 14.8 mm, JUE no. 15837-11. Figure 7. Right-valve hinge, hinge length 29.7 mm, JUE no. 15837-12. Figures 8, 9. Pallial sinus of both valves; Figure 8, length 43.6 mm+, JUE no. 15837-10; Figure 9, length 17.6 mm, JUE no. 15837-9. Figures 10–12. Outline of shells; Figure 10a, dorsal view showing long external ligament. Figure 10b, lateral view, length 35.4, JUE no. 15837-7; Figure 11, length 50.9 mm, JUE no. 15837-6; Figure 12, length 74.6 mm, JUE no. 15837-1.

shaped, approximately as deep as wide. Pallial line entire. The hinge dentition could not be examined fully. One specimen shows that the central of the three teeth of the right valve is bifurcated. A rather well-preserved specimen is 65 long and 40 mm high. Another, which is damaged at both ends, is 32 mm thick and 45 mm high.

The interior of the shell shows radial striations, which are well-visible in worn specimens” (Yokoyama, 1890).

**Redescription:** Shell of moderate size, attaining 74.6 mm length; shell outline elliptical, moderately inflated, equivalve and inequilateral, sculptured by

irregular growth lines. Beak prosogyrate, situated at anterior fifth of shell. Anterodorsal margin broadly arched, graduating into rather straight and oblique anterior margin; ventral margin broadly arcuate; postero-dorsal margin nearly straight, forming obtuse angle with rounded posterior margin. Escutcheon demarcated by blunt ridge running from beak to posterior end; lunule absent. External ligament strong and occupying two-fifths of posterior length.

Hinge plate rather wide, with three cardinal teeth in each valve. Right valve hinge: anterior cardinal tooth (3a) long, parallel to dorsal margin; posterior cardinal tooth (3b) vertical, stout, bifid, connected to anterior tooth above central tooth; area behind posterior cardinal tooth deeply excavated; posterior nymphal ridge low but distinct; central tooth (1) thin and long, nearly parallel to the anterior one, inserting its top under dorsal teeth (3a, b); subumbonal pit long and shallow just below umbo. Left valve hinge: anterior tooth (2a) long, parallel to antero-dorsal margin, connected to short central tooth (2b); posterior tooth (4b) thin, oblique posteriorly, separated from central tooth by deep groove; subumbonal pit deeply excavated, situated above posterior tooth.

Anterior muscle scar subcircular; posterior one pear-shaped; pallial sinus shallow, as wide as deep; strong ridge running from beak to deepest point of pallial sinus; radial interior striae rather weak.

**Comparison:** *Hubertschenckia* is currently only known from its type species *H. ezoensis*. The most closely related species are found in the genus *Archivesica*: *A. kawamurai* (Kuroda, 1943) and *A. georgemoorei* n. sp. described herein. *Hubertschenckia ezoensis* resembles *A. kawamurai* in having a bifid posterior cardinal tooth and a thin anterior cardinal tooth along the dorsal margin in the right valve, and in the existence of subumbonal pit and a shallow pallial sinus. However, *A. kawamurai* differs from *H. ezoensis* in having a more vertical central tooth (1) and a shorter anterior cardinal tooth (3a) in the right valve, a longer and anteriorly inclined central tooth (2b) and a shorter posterior tooth (4b) in the left valve; a smaller and deeper subumbonal pit, and strongly impressed radiating interior striae. The extant species *Archivesica solidissima* (Okutani, Hashimoto & Fujikura, 1992) was recently synonymized with *A. kawamurai* based mainly on molecular data (Kojima et al., 2006).

The hinge of *Archivesica georgemoorei* resembles that of *H. ezoensis* in having a bifid posterior cardinal tooth in the right valve (3b) and a thick anterior cardinal (1) parallel to the dorsal shell margin. It differs significantly, however; in having a more posteriorly directed posterior cardinal (3) in the right valve, and a thinner posterior cardinal (4), a smaller anterior cardinal (2) in

the left valve, and the nymph is shorter in *Archivesica georgemoorei*.

**Remarks:** Yokoyama (1928) described *Meretrix (Macrocallista) ezoensis* (Yokoyama) from the Pliocene-Pleistocene "upper Byoritsu Bed" in Taiwan. However, as noted by Takeda (1953), the hinge and shell morphology is distinctly different from *Hubertschenckia ezoensis*. Honda (1989) described two articulated specimens from an *Ostrea*-bearing sandstone of the Eocene Shitakara Formation in eastern Hokkaido as *Hubertschenckia ezoensis*, but did not illustrate their hinge structures. From their mode of occurrence, we infer that these specimens were shallow water-dwelling venerids rather than vesicomyids.

**Distribution:** Upper Eocene Poronai Formation in the Yubari coal-field, central Hokkaido; upper Eocene? Tappu Formation in the Uryu coal-field, northwestern Hokkaido (Ohara & Kanno, 1969, 1973); upper Eocene Omagari Formation and lower Oligocene Nuibetsu Formation (Takeda, 1953) in the Kushiro coal-field, eastern Hokkaido.

#### Genus *Adulomya* Kuroda, 1931

?*Pleurophopsis* Van Winkle, 1919:23.

*Adulomya* Kuroda, 1931:27.

*Ectenagena* Woodring, 1938:51.

**Type species:** *Adulomya uchimuraensis* Kuroda, 1931 (by monotypy); Miocene Bessho Formation, central Honshu, Japan.

**Redefinition:** Shell thin, large, elongate or cylindrical, ventral margin concave or almost straight; both ends rounded; beaks prosogyrate, situated anteriorly; surface with coarse, concentric growth increments. Inner surface with deep anterior muscle scar bounded by a deep groove; posterior muscle scar indistinct. Interior of ventral margin thick, with numerous fine radial riblets. Ligament external and long. Left valve with strong posterior cardinal (4b) parallel or oblique to posterior shell margin; anterior cardinal strong, 2b points ventrally, 2a parallel or subparallel to the antero-dorsal margin; nymph short. Right valve with two cardinals, anterior tooth (1) weaker than posterior one, pointing in an antero-ventral direction, posterior tooth (3b) pointing in a postero-ventral direction. Subumbonal pit in both valves present or in some cases absent (modified from Kanno et al., 1998).

**Remarks:** Because he had only a few articulated specimens at hand, Kuroda (1931) erroneously described *Adulomya uchimuraensis* as edentulous and consequently placed the genus in the protobranch family Solemyidae Adams & Adams, 1857. When Kanno & Ogawa (1964) allocated *Adulomya chitanii*



Kanehara, 1937 to *Akebicoucha* (= *Archivesica*), they emphasized the edentulous hinge of *A. uchiuuraensis*. *Adulouya* was subsequently treated as solemyid by Kamada (1962), Cox et al. (1969), and Boss & Turner (1980), among others.

However, Habe (1977) had already described the strong cardinal teeth and the absence of a pallial sinus in *A. uchiuuraensis* and placed *Adulomya* in the Vesicomidae. Kanno et al. (1998) used many newly collected specimens of *Adulouya uchiuuraensis* from one of the localities described by Kuroda (1931) to redefine *Adulouya*. They pointed out that *Adulouya* shares almost all its characters with *Ectenagea*, but differs by its subumbonal pit which is present throughout the entire ontogeny of the shell, whereas in *Ectenagea* the subumbonal pit is supposedly present only in juveniles. This distinction, however, is doubtful. The holotype of *Calyptogena elongata* Dall, 1916, type species of *Ectenagea* has a subumbonal pit judging from the figures provided by Boss (1968). Kanno et al. (1998) noted that the holotype with a shell length of 43 mm is a young specimen, but Coan et al. (2000) gave its maximum length as 50 mm. Thus, *Ectenagea* is here regarded as a synonym of *Adulouya*.

*Pleuophopsis* Van Winkle, 1919, from the middle Miocene of Trinidad (Caribbean) resembles *Adulouya* in all known characters, but its type species *P. uniooides* Van Winkle, 1919, is only known from incomplete specimens that lack crucial characters including cardinal tooth 3b, escutcheon, and nymph. Therefore the name *Pleuophopsis* should not be used (Kiel, 2007). Other species assigned or referred to *Pleuophopsis* may be vesicomids, but do not belong to *Adulouya* (Kiel & Peckmann, in press).

*Archivesica* resembles *Adulouya* in having three radiating cardinal teeth in the left valve and a subumbonal pit. It differs from *Adulouya* by having a narrow hinge plate, three cardinal teeth in the right valve, and a shallow pallial sinus. *Calyptogena* (s.s.) can easily be separated from *Adulouya* by its three cardinal teeth including a very stout right posterior one, and by the lack of a subumbonal pit.

**Included fossil species:** *Adulouya uchiuuraensis* Kuroda, 1931, *Adulomya chitani* Kanehara, 1937, *Calyptogena* (C.) *chiuokeensis* Squires & Goedert, 1991, and *Adulouya hokkaidoensis* Amano & Kiel, sp. nov.

**Distribution:** Recent species are known from vents and seeps in the northeastern Pacific (Coan et al., 2000; Desbruyès et al., 2006) and from seeps in the northwestern Pacific (Sasaki et al., 2005); fossil species are known from late Eocene seeps in Washington State (this study), from early to middle Miocene whale-falls in Japan (Amano & Little, 2005; Amano et al., 2007), and from a turbidity current deposit of early Oligocene

age in the Makah Formation in Washington State (Goedert & Squires, 1993).

*Adulomya hokkaidoensis* Amano & Kiel, sp. nov.

(Figures 13–18)

*Calyptogena* sp. Amano & Little, 2005:figs. 5 A, E, F.

**Diagnosis:** A medium-sized *Adulouya* with elongate shell, sculptured by rough concentric ridges; subumbonal pit very elongate; ligament exterior and short, two radiating cardinal teeth in right valve; left valve with three radiating teeth, middle one strongest.

**Holotype:** Length 46.2 mm, height 16.7 mm, JUE no. 15848.

**Paratype:** Length 59.4 mm, height 16.7 mm+, JUE no. 15849; Length 66.2 mm+, height 22.6 mm, JUE no. 15850.

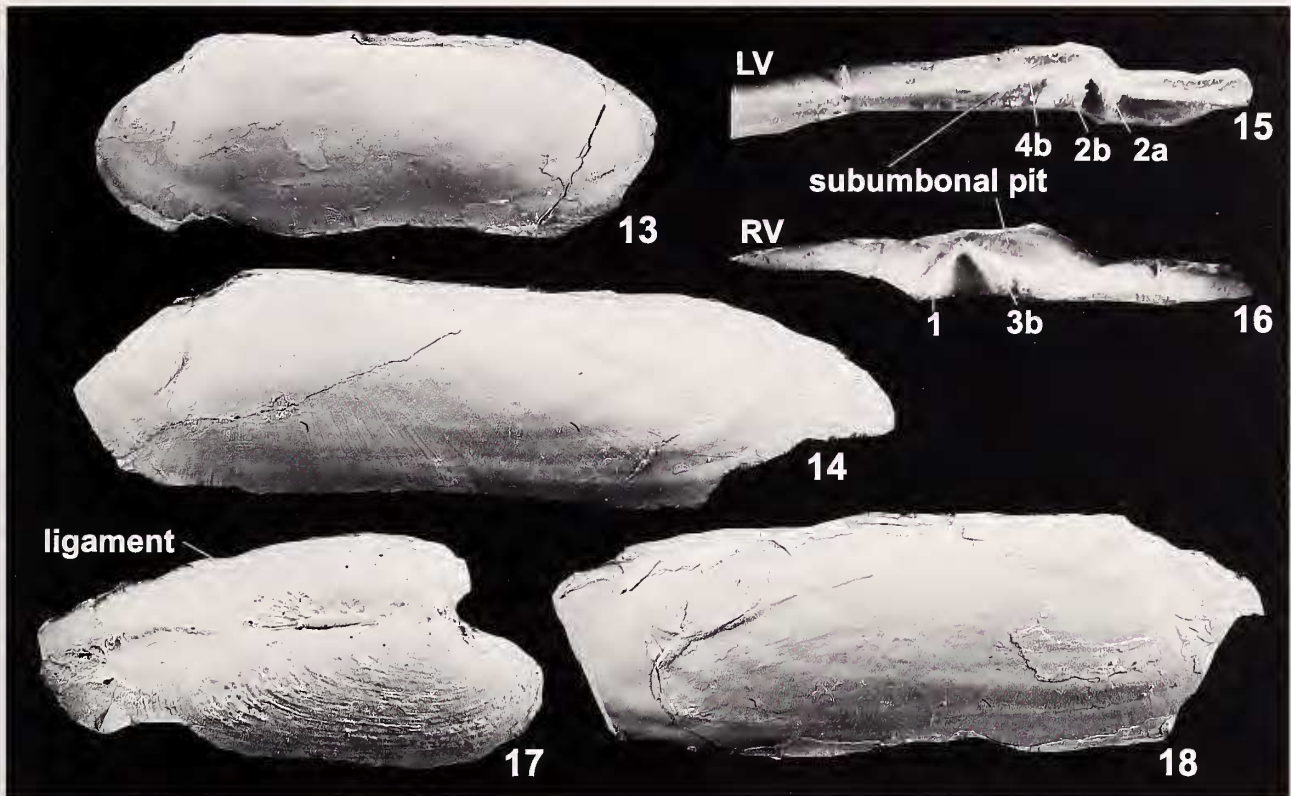
**Type locality:** Large road side cliff along the Setakinai River, 5.5 km upstream from Shosanbetsu Village, Hokkaido; lower middle Miocene Chikubutsu Formation.

**Description:** Shell of moderate size, more than 66.2 mm long, thin-walled, elongate, equivalve and inequilateral, weakly inflated, sculptured by few rough concentric ridges on posterior part, growth lines cover the entire surface. Beak prosogyrate, situated at anterior fifth of shell. Antero-dorsal margin broadly arched, graduating into rounded anterior margin; ventral margin straight and slightly excavated at middle portion; postero-dorsal margin nearly straight, parallel to ventral margin, graduating into rounded posterior margin. Escutcheon and lunule absent; ligament exterior, weak and short.

Hinge plate narrow, with two cardinals in right valve and three cardinals in left valve. Right valve hinge: anterior cardinal tooth (3a) reduced; posterior cardinal tooth (3b) slightly bifid, oblique posteriorly; central tooth (1) thin, anteriorly slightly oblique; subumbonal pit long and shallow just below umbo. Left valve hinge: anterior tooth (2a) thin, slightly oblique anteriorly, connected to stout middle tooth (2b); posterior tooth (4b) very thin, oblique posteriorly; subumbonal pit shallow, situated above posterior tooth.

Anterior muscle scar subcircular; posterior one ovate; pallial sinus absent; deep groove running just under posterior muscle scar; radial interior striae distinct.

**Comparison:** The extant species *Adulouya elongata* (Dall, 1916) resembles *A. hokkaidoensis* in having a thin and compressed shell with two cardinal teeth in the



Figures 13–18. *Adulomya hokkaidoensis* sp. nov. Figure 13. Holotype, length 46.2 mm, JUE no. 15848. Figure 14. Paratype, length 59.4 mm, with slightly broken ventral part, showing distinct radiating interior striae, JUE no. 15849. Figure 15. Rubber cast of left valve hinge of paratype (JUE no. 15849), hinge length 25.7 mm. Figure 16. Rubber cast of left valve hinge of paratype (JUE no. 15851), hinge length 16.5 mm. Figure 17. Paratype, dorsal view showing the short ligament, length of specimen 40.8 mm+, JUE no. 15852. Figure 18. Paratype showing entire pallial line and posterior adductor scar, length 66.2 mm+, JUE no. 15850.

right valve, a subumbonal pit and lacking a pallial sinus. However, its more elongate shape and the presence of concentric undulations on the posterior surface distinguish *A. hokkaidoensis* from *A. elongata*. The fossil *A. uchimuraensis* and the extant *A. phaseoliformis* (Métivier, Okutani & Ohta, 1986) have larger and more elongate shells.

**Distribution:** Known only from the whale-fall community at the type locality.

**Etymology:** For its occurrence on Hokkaido.

*Adulomya chinookensis* (Squires & Goedert, 1991)

(Figures 19–23)

*Calyptogena* n. sp. Goedert & Squires, 1990:figs. 2 o–p.

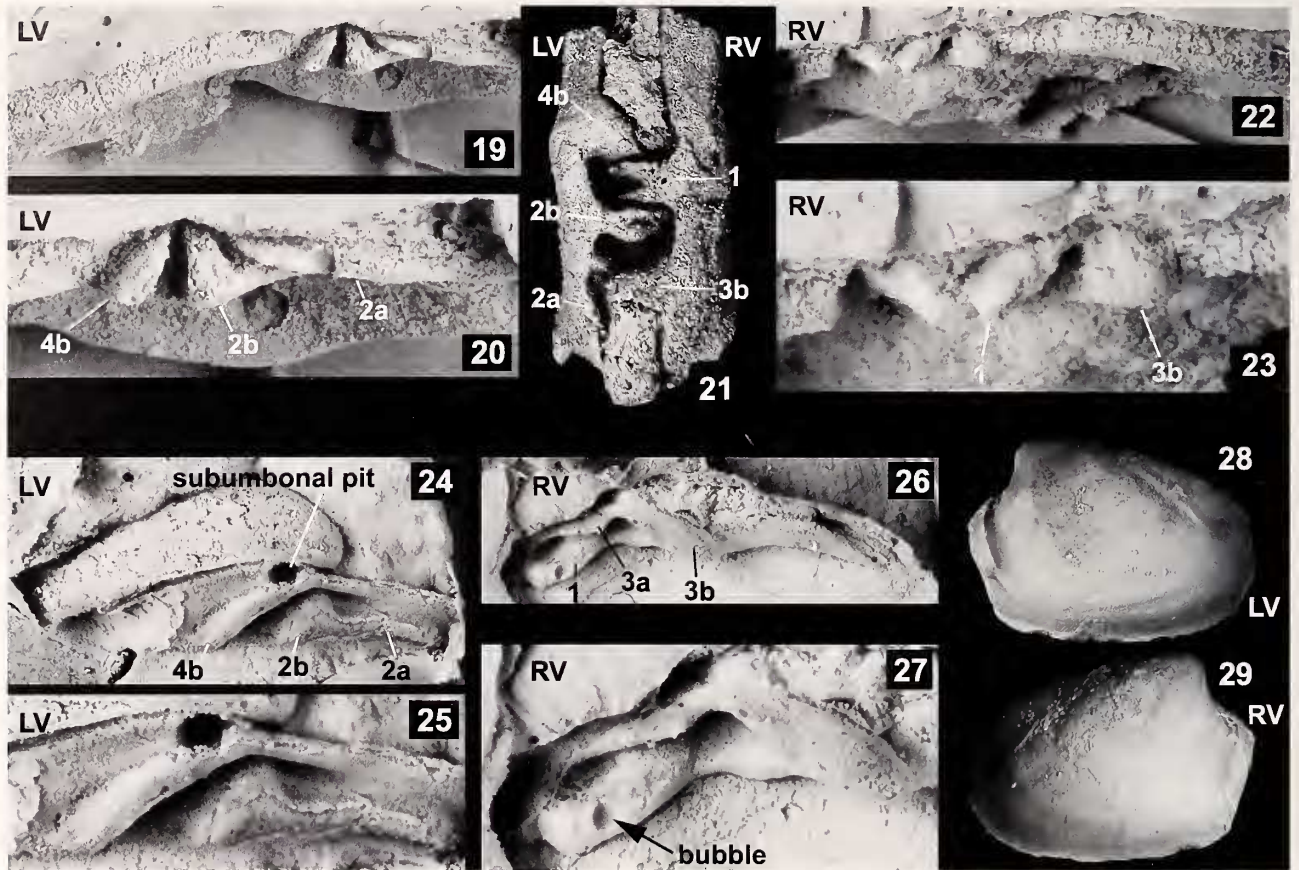
*Calyptogena (Calyptogena) chinookensis* Squires & Goedert, 1991:413–415, figs. 2.7–2.11; Goedert & Squires, 1993:74–76, fig. 3.

*Vesicomya (Calyptogena)* sp. Goedert et al., 2003:228, Pl. 42, figs. 6, 7.

non *Calyptogena (Calyptogena) chinookensis* Squires & Goedert. Goedert & Squires, 1993:fig. 4.

**Supplementary description:** Left-valve hinge with strong posterior cardinal (4b) pointing in postero-ventral direction, slightly tapering at its dorsal side; cardinal 2b solid, same length as cardinal 4b, pointing in ventral direction, anterior cardinal 2a detached from 2b, thinner than the other cardinals, elongate, and pointing in anterior direction. Right valve hinge with two cardinals, middle cardinal 1 elongate-lenticular, pointing in anterior direction, posterior cardinal 3b strong, bifid, peg-like, pointing in ventral direction. Pallial line entire, starting at postero-ventral end of anterior adductor scar, distant from ventral margin (ca. 22% of shell height below umbo, 44% at posterior turning point), no pallial sinus but pallial line merges with the elongate posterior adductor scar.

**Remarks:** Specimens previously assigned to *Calyptogena (Calyptogena) chinookensis* from various formations apparently belong to more than one species. Figures 19, 20, 22, and 23 show a silicone rubber cast of an internal mold of a specimen from the type locality at Bear River (LACMIP loc. 5802), which we consider to represent the ‘true’ *chinookensis*. Its right valve hinge



Figures 19–29. *Adulomya chinookensis* (Squires & Goedert, 1991) from the type locality at Bear River, Washington State, USA (LACMIP loc. 5802). Figures 19–20. Rubber cast of a steinkern (USNM 534948), left valve. Length of section shown in Figure 19:24.0 mm; close-up in Figure 20:13.0 mm. Figure 21. Ventral view of a complete, articulated hinge, length 14.0 mm (USNM 534949). Figures 22–23. Right valve of same rubber cast as in Figures 19–20, length of section shown in Figure 22:24.0 mm, close-up in Figure 23:11.0 mm.

Figures 24–29. *Archivesica* cf. *tschudi* (Olsson, 1931) from the Humptulips River, Washington State, USA. Figures 24–25. Rubber cast of an external mold of a left valve, note deep subumbonal pit, length of section shown in Figure 24: 12.0 mm, close-up in Figure 25: 8.0 mm (USNM 534950). Figures 26–27. Rubber cast of an external mold of a right valve, note that the round hole in the anterior side of cardinal 1 is a bubble in the rubber, not a shell feature. Length of section shown in Figure 26: 15.0 mm; close-up in Figure 27: 8.0 mm (USNM 534951). Figures 28–29. Steinkern from CSUN loc. 1583 showing pallial line and adductor scars, length 27.0 mm (USNM 534952).

differs from the late Oligocene specimen figured by Goedert & Squires (1993:fig. 4) because the cardinals 1 and 3 are not fused in the 'true' *chinookensis*, and cardinal 1 is more elongate than in Goedert & Squires's specimen. Additional material collected at the same site from which Goedert & Squires (1993) described their right valve showed that the corresponding left valve differs even more from that of the 'true' *chinookensis* by having a thick, roundish cardinal 2b and an elongate, thin cardinal 2a. The late Oligocene species to which the right valve figured by Goedert & Squires (1993:fig. 4) belongs, is described as *Archivesica knapptonensis* n. sp. below. Specimens described as *Vesicomya* (*Calypptogena*) sp. by Goedert et al. (2003) from the 'Whiskey Creek site' in the Pysht Formation (late Eocene,

Washington State) have the same hinge dentition as the Bear River specimens shown here, but have a stronger ridge from the umbo to the posterior adductor scar on the inner side of the shell.

**Distribution:** Upper Eocene informal 'Siltstone of Cliff Point' (i.e., Bear River deposit) and the 'Whiskey Creek site' in the Pysht Formation to the lower Oligocene Makah Formation, Washington State, USA. The species is probably more widely distributed in this area, but specimens with the same general shell outline apparently belong to different species and genera, and without the hinge, except at the type locality of *chinookensis*, we are unable to confirm any additional records.

Genus *Archivesica* Dall, 1908

*Archivesica* Dall, 1908:418.

*Phreagena* Woodring, 1938:50.

*Akebiconcha* Kuroda, 1943:17.

**Type species:** *Callocardia gigas* Dall, 1896 (by original designation); Recent, Gulf of California.

**Original diagnosis:** Shell inflatedly modioliform, medially slightly constricted, with the hinge plate short and broad and the hinge teeth radially disposed; lunule not circumscribed by an impressed line; pallial line without a sinus, but descending nearly vertically from the middle of the posterior adductor scar (Dall, 1908, p. 418).

**Emended diagnosis:** Shell broadly oval to very elongate; sculpture of commarginal growth lines only; lunular incision present or absent; anterior adductor scar moderately deep impressed, anterior adductor scar only weakly impressed; pallial line with shallow sinus. Hinge of right valve with subumbonal pit; anterior cardinal tooth thin, parallel or somewhat oblique to antero-dorsal margin; middle cardinal tooth (1) as strong as 3a or much thicker, starting anywhere between underneath umbo; posterior cardinal tooth (3b) sometimes bifid, as strong as 3a or stronger, usually fused with 3a underneath umbo, either perpendicular to 3a or points in a more posterior direction. Hinge of left valve with subumbonal pit, anterior cardinal 2a elongate and thin, and parallel or subparallel to antero-dorsal margin; middle cardinal 2b stout, peg-like tooth of variable thickness; posterior cardinal 4b usually thin and long.

**Comparison:** *Calyptogena* differs from *Archivesica* by the presence of a nymphal ridge in the right valve, which *Archivesica* mostly lacks (Figure 5); by the lack of a subumbonal pit, which is present in *Archivesica*; by the orientation of the anterior branch of the cardinal tooth 3b, which points in a ventral or even anterior direction in *Calyptogena*, but points in a posterior direction in *Archivesica*; and by the large size of cardinal 3b of *Calyptogena* which is much smaller in *Archivesica*. Moreover, the shell size of *Calyptogena* is usually small (about 60 mm in maximum length) and does not exceed 90 mm (cf. Krylova and Sahling, 2006), whereas the maximum size of many Recent species of *Archivesica* exceeds 100 mm. *Adulomya* lacks an anterior cardinal 3a, which distinguishes it from *Archivesica*. *Hubertschenkia* differs from *Archivesica* by its much stronger cardinals 3a and 3b and also by the orientation of the anterior branch of the cardinal tooth 3b, which points in a ventral or slightly anterior direction. In *Archivesica*, 3b points in a posterior direction. The genus *Vesicomya* apparently consists of

small species from the Atlantic (Cosel & Salas, 2001), and differs from *Archivesica* in having much smaller, thinner, roundish shells (up to 13 mm in length), cardinal teeth parallel to the hinge line, no pallial sinus, and no subumbonal pit (e.g., Figure 5).

**Remarks:** Okutani et al. (2000) reviewed the nomenclatural history of *Archivesica*, largely agreed with Dall's original diagnosis, and agreed with Bernard (1974) that there may be a small pallial sinus. Here we provide a more detailed diagnosis of the configuration of the hinge teeth and show that there can be a lunular incision (= a groove between a non-depressed lunule and disc), contrary to Dall's diagnosis. Cosel & Salas (2001) showed for the vesicomid genera *Vesicomya* and *Isorropodon* that the lunular incision can vary greatly in strength from nearly absent to deeply incised. We consider the presence or absence of a lunular incision insufficient to distinguish genera among the Vesicomidae and emend Dall's diagnosis accordingly.

The molecular phylogenetic tree of vesicomids of Kojima et al. (2004) derived from mitochondrial COI sequences included a monophyletic group of eight species that included *Archivesica gigas*, the type species of *Archivesica*, and *A. solidissima*, which was shown to be a synonym of *A. kawamurai* Kuroda, 1943 (Kojima et al., 2006), type species of *Akebiconcha* Kuroda, 1943. Thus we consider *Akebiconcha* to be a synonym of *Archivesica*. All eight taxa of this monophyletic group were assigned to *Archivesica* by Sasaki et al. (2005).

Woodring (1938) introduced *Phreagena* based on *P. lasia* Woodring, 1938 but later recommended to synonymize this genus with *Calyptogena* (cited in Winterer & Durham, 1962; Boss, 1968; and Boss & Turner, 1980). These authors as well as Squires (1991) followed this synonymization, but Krylova & Janssen (2006) attempted to revive *Phreagena* and suggested close phylogenetic relations to *Akebiconcha* and *Archivesica*. As outlined above, we consider *Akebiconcha* to be synonymous with *Archivesica*. Also *Phreagena lasia* shows (on the illustrations of Woodring, 1938, pl. 5, fig. 3; and Squires, 1991:fig. 8; and perhaps also of Krylova & Janssen, 2006, pl. 2, fig. 7) a bifurcating central cardinal 1, a character that we have not seen in our material of *Archivesica*. However, the central cardinal 2b in species of *Adulomya* may or may not bifurcate (compare figs. 4E–G of Boss & Turner, 1980). Also, in their diagnosis of *Phreagena*, Krylova & Janssen (2006, p. 237) wrote that cardinal 1 is 'sometimes bifid.' Thus we consider a bifurcating central cardinal 1 to be insufficient to distinguish genera among the Vesicomidae and regard *Phreagena* as a synonym of *Archivesica*.

**Included fossil species:** *Archivesica georgemoorei* n. sp. (Oligocene?), *Archivesica knapptonensis* n. sp. (late Oligocene), *Archivesica* cf. *tschudi* (Olsson, 1931) (late

middle Eocene, see below), *Phreagena gibbera* Crickmay, 1929 (*P. lasia* Woodring, 1938 has been considered to be a junior synonym of *P. gibbera* by Squires, 1991; early Pliocene to middle Pleistocene), *Calypptogena nipponica* Oinomikado & Kanehara, 1938 (late Miocene to Pliocene), and *Akebiconcha kawamurai elongata* Ozaki, 1958 (late Pliocene).

**Distribution:** Recent species occur at vents and seeps in the Pacific (Scarlato, 1981; Coan et al., 2000; Sasaki et al., 2005), fossil species first appear at seeps in the late middle Eocene of Washington and are also known from seep deposits in California, Washington, Alaska, and Honshu (this study).

*Archivesica* cf. *tshudi* (Olsson, 1931)

(Figures 24–29)

*Vesicomya* sp. Squires & Goedert, 1996:270; Goedert & Kaler, 1996:67.

?*Vesicomya tshudi* Olsson, 1931:54, pl. 4., figs. 6, 8.

?*Vesicomya ramondi* Olsson, 1931:55, pl. 4, fig. 3.

?*Vesicomya* (*V.*) aff. *V.* (*V.*) *tshudi* Olsson. Squires & Gring, 1996:69, figs. 4.9–4.12.

**Description:** Shell small and ovate; postero-dorsal margin almost straight, angulate at transition to subtruncated posterior margin; ventral margin slightly arcuated. Umbo protruded above dorsal margin; beak situated anterior at one-seventh of shell length. Anterior adductor scar deeply impressed, pallial line starting at postero-ventral end of anterior adductor scar, moderately distant from ventral margin, no pallial sinus. Right valve with very strong middle cardinal (1), parallel to shell margin, slightly longer in anterior direction than anterior cardinal (3a); anterior cardinal (3a) thin, somewhat undulating, parallel to shell margin; posterior cardinal (3b) bifurcate, anterior branch slightly concave, as thin as 3a, posterior branch elongate-lenticular, almost as strong as cardinal (1),

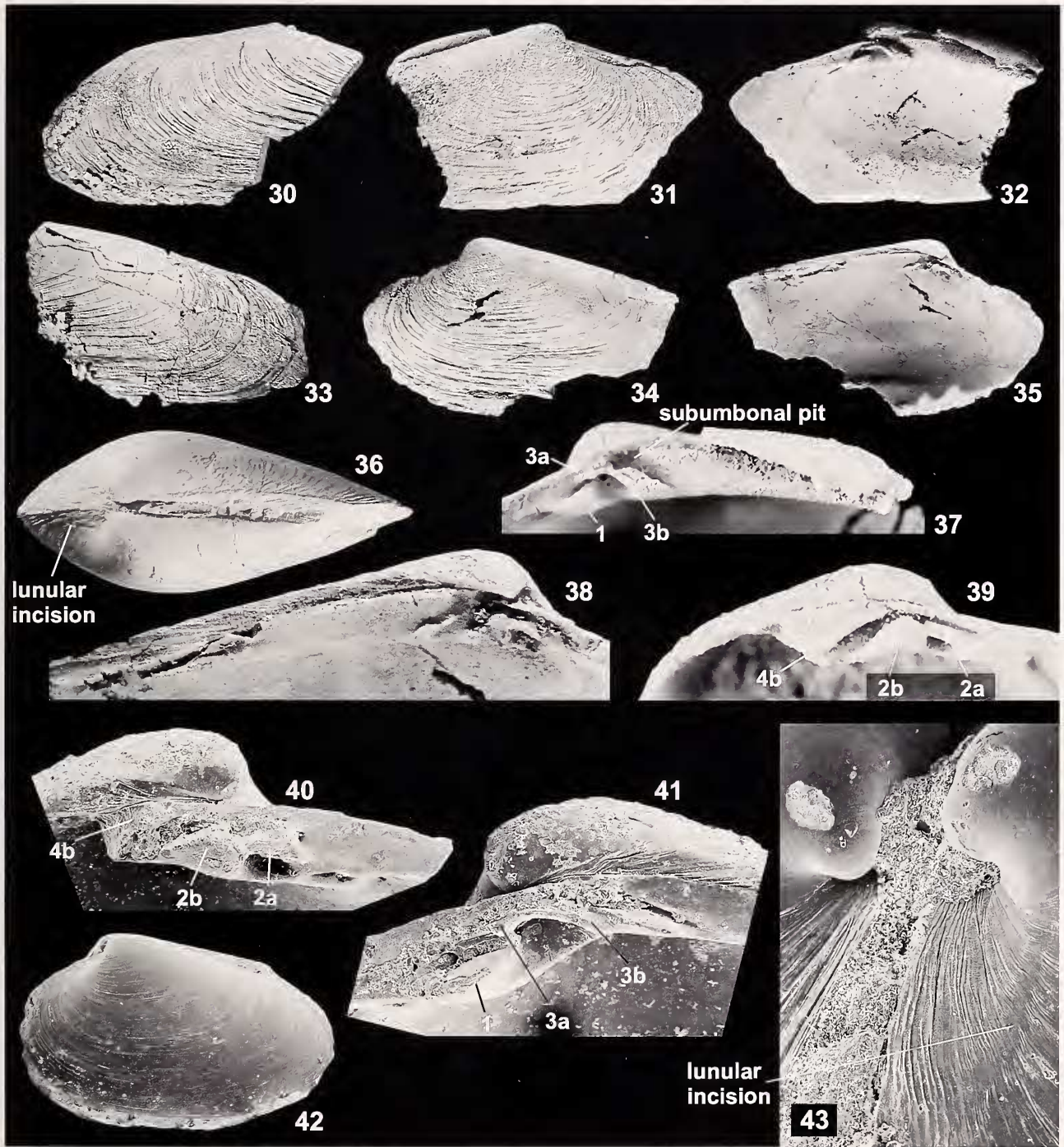
both branches point in a postero-ventral direction; nymph narrow, slightly shorter than hinge tooth area. Right valve with thin, elongate, undulating anterior cardinal (2a) parallel to shell margin, fused with cardinal 2b beneath umbo, 2b thick, short, comma-shaped, almost parallel to shell margin but slightly tilted in a ventral direction; posterior cardinal (4a) thin, straight, parallel to shell margin, fused with 4b just posterior of umbo, posterior cardinal 4b strong, elongate, slightly convex, pointing in a postero-ventral direction; subumbonal pit very deep and almost round.

**Remarks:** Our specimens show no difference in general shell shape and pallial-line characters to those described and illustrated as *V. tshudi* and *V. aff. tshudi* by Olsson (1931) and Squires & Gring (1996). Olsson (1931, p. 55) noted impressions of the hinge-line show two cardinal teeth in each valve and no laterals. This generally agrees with the observations on our material, but does neither allow an unequivocal recognition of, nor a clear distinction from, '*Vesicomya*' *tshudi*. Thus we describe the species here as *Archivesica* cf. *tshudi*. It is currently the oldest vesicomimid for which hinge dentition is known.

Olsson (1931) described *Vesicomya tshudi* and *Vesicomya ramondi* without discussing distinguishing features. According to his descriptions, *ramondi* has a pointed posterior margin, whereas that of *tshudi* is rounded. Squires & Gring (1996) noted that *ramondi* is more elongate than *tshudi*. However, Olsson's figures of *ramondi* (pl. 4, fig. 3) and his paratype of *tshudi* (pl. 4, fig. 8) show no discernable difference. Considering the intraspecific variability among our specimens from the Humptulips Formation, we think it is more likely that *tshudi* and *ramondi* are the same species.

**Distribution:** Humptulips Formation, Washington State, USA, upper middle Eocene (Squires & Goedert, 1996; herein). Specimens with identical shell shape but unknown hinge details were described as *Vesicomya* aff. *tshudi* from the upper Eocene Wagonwheel

Figures 30–43. *Archivesica knapptonensis* n. sp. from the upper Oligocene part of the Lincoln Creek Formation in Washington State, USA. Specimens on Figures 30–39 coated with ammonium chloride; specimens on Figures 40–43 coated with gold for SEM photography. Figure 30. Fragment of right valve, posterior side, from Knappton (LACMIP loc. 5843), length 18.0 mm (USNM 534953). Figures 31–32. Holotype, internal and external view of right valve, from Knappton (LACMIP loc. 5843), length 13.5 mm (USNM 534954). Figure 33. Fragment of posterior side of left valve, from Knappton (LACMIP loc. 5843), length 20.0 mm (USNM 534955). Figures 34–35. Paratype, internal and external view of left valve, from LACMIP loc. 5843, length 19.0 mm (USNM 534956). Figure 36. Ventral view of an articulated specimen, showing the well-developed lunular incision, from LACMIP loc. 17747b, length 23.0 mm (USNM 534957). Figure 37. Close-up of hinge dentition of holotype. Figure 38. Close-up on hinge dentition of paratype (same specimen as Figures 34–35). Figure 39. Close-up of hinge dentition of a left valve of a smaller specimen than in Figure 38, from LACMIP loc. 5843, length 11.0 mm (USNM 534958). Figures 40–43. Small specimens from the 'Canyon River site,' note that the posterior branch of the bifurcating cardinal 3b is more detached from 3a than in the larger specimens shown above. Figure 40. Close-up on hinge of left valve, length of section 2.1 mm (USNM 534959). Figure 41. Close-up of hinge of right valve, length of section 2.0 mm (USNM 534960). Figure 42. Left valve of articulated specimen, length 5.3 mm (USNM 534961). Figure 43. Close-up on the anterodorsal area of the specimen as in Figure 42, arrow indicates lunular incision, length of section 0.95 mm.



Figures 40–43. Small specimens from the ‘Canyon River site,’ note that the posterior branch of the bifurcating cardinal 3b is more detached from 3a than in the larger specimens shown above. Figure 40. Close-up on hinge of left valve, length of section 2.1 mm (USNM 534959). Figure 41. Close-up of hinge of right valve, length of section 2.0 mm (USNM 534960). Figure 42. Left valve of articulated specimen, length 5.3 mm (USNM 534961). Figure 43. Close-up on the anterodorsal area of the specimen as in Figure 42, arrow indicates lunular incision, length of section 0.95 mm.

Formation in California, USA (Squires & Gring, 1996); the original *Vesicomya tshudi* is from outcrops in the upper Oligocene (Chattian) 'Pleuophopsis zone' in the Heath Formation in northern Peru, which have recently been identified as hydrocarbon seeps (Kiel & Peckmann, in press).

*Archivesica knapptonensis* Amano & Kiel, sp. nov.

(Figures 30–43)

*Calypptogena (Calypptogena) chinookensis* Squires & Goedert. Goedert & Squires, 1993:74, fig. 4.

**Diagnosis:** A small-sized *Archivesica* with elongate shell sculptured by fine irregular concentric lines and with short anterior cardinal tooth in right valve.

**Holotype:** Fragment of right valve with preserved hinge dentition, length 13.5 mm+, height 7.0 mm, USNM 534954.

**Paratypes:** USNM 534956, fragment of left valve with preserved hinge dentition, length 19.0 mm+, height 11.0 mm; USNM 534956, fragment of left valve with preserved hinge dentition, length 11.0 mm+, height 7.0 mm; LACMIP 12097, fragment of right valve with hinge dentition, length 8.8 mm.

**Type locality:** LACMIP loc. 5843, beach terrace of the Columbia River near Knappton, Washington State, USA; upper Oligocene part of the Lincoln Creek Formation.

**Description:** Shell small, elongate and little inflated; escutcheon elongate and narrow; lunular incision well developed, elongate; postero-dorsal margin almost straight, angulate at transition to pointed posterior margin; ventral margin straight or slightly convex, anterior margin pointed but evenly rounded. Sculpture of irregular commarginal growth lines only. Pallial line pallial line starting at postero-ventral end of anterior adductor scar, not discernable in posterior part of shell. Right valve hinge with thick, blunt middle cardinal (1), slightly concave, subparallel to shell margin, its posterior half situated below anterior cardinal (3a); anterior cardinal (3a) very short, thin, parallel to shell margin; posterior cardinal (3b) bifurcate, pointing in a postero-ventral direction. Left valve with moderately thick, straight anterior cardinal (2a) parallel to shell margin; middle cardinal (2b) very thick, peg-like, pointed at its posterior side; posterior cardinal (4b) elongate, slightly thinner than 2a, slightly convex, pointing in a postero-ventral direction. Subumbonal pit oval and well developed in right valve, much smaller in left valve. Nymph elongate, about twice as long as hinge tooth area. Anterior adductor scar moderately deep impressed, pear-shaped. Anterior pedal retractor

scar deeply impressed, positioned between anterior cardinal tooth and anterior adductor scar.

**Comparison:** As far as we know, this is by far the most elongate fossil *Archivesica*. The Recent Japanese *A. laubieri* (Okutani & Metivier, 1986) is similar to *A. knapptonensis* in having an elongate outline, fine irregular concentric lines, and a thin anterior cardinal tooth (3a). *Archivesica laubieri* has a much larger shell and a shorter nymph than *A. knapptonensis*. Another Recent Japanese species, *Archivesica tsubasa* Okutani, Fujikura & Kojima, 2000 is even more elongate than *A. knapptonensis* and has a similarly long nymph. It differs from *A. knapptonensis* by the complete absence of a lunular incision, a very short cardinal 3a and a non-bifurcating cardinal 3b in the right valve. *Archivesica tsubasa* also grows to a much larger size (up to 212 mm in length) than any of the fossil specimens reported herein. The type species *A. gigas* differs from *A. knapptonensis* in having a broader, less elongate shell, a proportionally shorter nymph, the cardinal tooth 2b of the left valve has a broader base, and cardinal tooth 3b of the right valve is slightly concave and does not appear to bifurcate.

**Distribution:** Upper Oligocene cold seep deposits of the Lincoln Creek Formation, Washington State, USA.

**Etymology:** After the vanished town of Knappton near the type locality. Knappton was founded by Jabez B. Knapp soon after the end of the U. S. Civil War and first thrived on a cement plant that most likely used seep limestone. Later the town was supported by timber. It had a post office from 1871 to 1941, and rapidly declined after the sawmill burned down in 1941.

*Archivesica georgemoorei* Amano & Kiel, sp. nov.

(Figures 44–49)

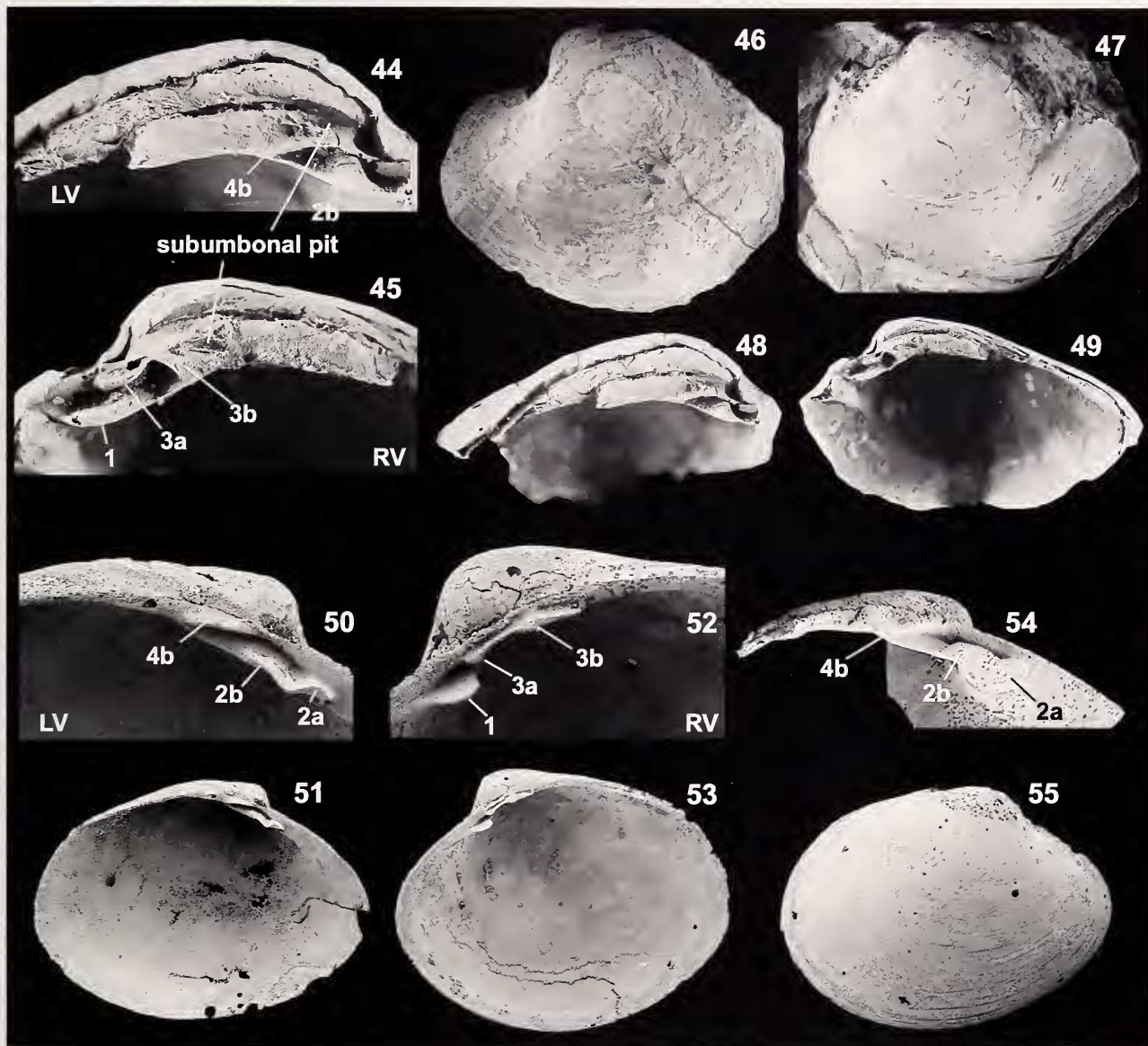
“new genus of Vesicomidae” Moore, 1969:A32.

**Diagnosis:** A medium-sized *Archivesica* with oval shell and with very short anterior cardinal tooth in left valve.

**Holotype:** Internal mold, length 46 mm+, height 35 mm, UCMP 55517, we figure rubber casts of each valve.

**Paratypes:** Six specimens from the type locality (USGS loc. M1755), figured specimens include UCMP 55519 (left valve, length 48.5 mm, height 43.0 mm), and UCMP 55520 (left valve, length 48.0 mm, height 38.0 mm).

**Type locality:** USGS loc. M1755; about 300 m below the top of the Sitkalidak Formation in the type area at 57°11.1'N, 152°56.6'W, on the north shore near the



Figures 44–49. *Archivesica georgemoorei* n. sp. from the Sitkalidak Formation on Sitkalidak Island, Alaska, USA (USGS loc. M1755), all specimens coated with ammonium chloride. Figures 44–45, 48–49. Rubber casts of the holotype, UCMP 55517. Figures 45, 49. Right valve, length 47.0 mm. Figures 44, 48. Left valve, length 35.0 mm. Figure 46. Paratype, UCMP 55519, external view of left valve, length 48.5 mm. Figure 47. Paratype, UCMP 55520, external view of left valve, length 48.0 mm.

Figures 50–55. *Isorropodon frankfortensis* n. sp. from the Astoria Formation in Washington State, USA (USGS loc. M2790), all specimens coated with gold for SEM photography. Figures 50–51. Paratype, interior of left valve and close-up of hinge, length 3.2 mm (USNM 534962). Figures 52–53. Holotype, interior of right valve and close-up of hinge, length 3.3 mm (USNM 534963). Figure 54. Left valve hinge of a fragment of a large specimen, length 1.6 mm (USNM 534964). Figure 55. Exterior of a right valve, length 3.5 mm (USNM 534965).

east end of Sitkalidak Island, Alaska; Oligocene(?) part of the Sitkalidak Formation.

**Description:** Shell medium size, oval and moderately inflated; beak prominent, prosogyrate, slightly anterior of midline; escucheon present; sculpture of weak irregular commarginal growth lines only, no postero-

dorsal ridge. Hinge moderately broad, teeth positioned below to slightly anterior of umbo. Right valve hinge with strong, elongate ventral cardinal (1) parallel to hinge margin, its posterior half situated under anterior dorsal cardinal (3a); anterior dorsal cardinal (3a) thin, elongate, slightly concave, subparallel to antero-dorsal margin; posterior dorsal cardinal (3b) rather thick.



bifid, pointing in a postero-ventral direction. Left valve hinge with long, thin, and slightly convex posterior cardinal (4b) pointing in a postero-ventral direction; above middle cardinal it seems to fuse with what could be the anterior cardinal (2a); middle cardinal (2b) stout, slightly pointed on anterior side. Nymph almost as long and broad as hinge teeth area; subumbonal pit present in both valves. Pallial line unknown.

**Comparison:** This species was reported as 'a new genus of Vesicomidae' by Moore (1969) but had never been described in detail. We think that the species can comfortably be placed in the genus *Archivesica* because it has a hinge dentition and subumbonal pit similar to the type species *A. gigas*. However, *A. georgemoorei* differs from other *Archivesica* species by its almost straight cardinal 1 in the right valve that runs parallel to the shell margin, in most other *Archivesica* species the posterior end of cardinal 1 points upwards to the beak. This feature also distinguishes *A. georgemoorei* from the type species. In addition, *A. gigas* has a higher cardinal 2b.

**Distribution:** Known only from the type locality.

**Etymology:** After the late Dr. George W. Moore (Corvallis, Oregon), who collected and first reported these shells.

#### Genus *Isorropodon* Sturany, 1896

*Isorropodon* Sturany, 1896:17.

**Type species:** *Isorropodon perplexum* Sturany, 1896 (by monotypy); Recent, north of Alexandria, eastern Mediterranean Sea.

**Remarks:** Cosel & Salas (2001) wrote that *Isorropodon* is distinguished from *Vesicomya* by its much larger and more oval to oval-oblong shell, the poorly developed or missing lunular incision, and the smooth valve margin without an incision. *Vesicomya* is smaller, the shells are very tumid to nearly spherical, and the general hinge-teeth configuration is the same. However, two of these 'distinguishing' characters appear to be not very distinctive. The lunular incision of *Vesicomya* was diagnosed by Cosel & Salas (2001) as very weak to well-defined, thus there seems to be little difference between 'very weak' (as in *Vesicomya*) and 'poorly developed' (as in *Isorropodon*). Also the difference in size appears to be gradual rather than distinctive: *Vesicomya* ranges from 3 to 13 mm in length, *Isorropodon* from 11.3 to 47 mm in length. The major difference between the two genera, and the reason why we keep them separate, is the ctenidium, which has two demibranchs in *Vesicomya*, but only one in *Isorropodon*. *Callogonia* has a similar shell outline but can easily be distinguished from *Isorropodon* based on its posterior area, its

obliquely truncate posterior margin, and the presence of a deep pallial sinus.

*Isorropodon frankfortensis* Amano & Kiel, sp. nov.

(Figures 50–55)

**Diagnosis:** A small *Isorropodon* with smooth and ovate shell, anterior margin slightly pointed; central cardinal 3a in right valve straight, very long, parallel to dorsal shell margin, nymph very narrow; lunular incision indistinct or absent.

**Holotype:** Length 3.3 mm, height 2.7 mm, USNM 534963.

**Paratype:** Length 3.2 mm, height 2.4 mm, USNM 534962.

**Type locality:** USGS loc. M2790, near Frankfort on the north shore of Columbia River, Wahikaikum County, Washington State, USA; lower Miocene part of the Astoria Formation.

**Description:** Shell small, attaining 10.5 mm in length, ovate and moderately inflated; beak prosogyrate, slightly elevated, in subcentral position; no lunular incision. Shell surface smooth with very fine growth increments. Hinge plate narrow, right valve with cardinal 1 just anterior of beak, thin, elongate, and parallel to dorsal shell margin; cardinal 3a commencing just below anterior margin of beak, elongate and very thin, slightly thickened anteriorly, parallel to dorsal shell margin, bends slightly ventrally at its posterior end; cardinal 3b just posterior of 3a and equally thin, slightly oblique toward dorsal shell margin, dipping down at the posterior side. Left valve: Cardinal 4b thin, subparallel to dorsal shell margin, 2a and 2b fused, slightly thicker than 4b but still thin, posterior part (presumably 2b) convex, anterior part (presumably 2a) slightly thicker, pointing slightly dorsally. In larger specimens, 4b more ventrally inclined and thicker, 2a and 2b shorter, more compact, and much thicker. Pallial line and sinus indistinct.

**Comparison:** Cosel & Salas (2001) reviewed and redescribed the Recent Atlantic species of *Isorropodon* in great detail. *Isorropodon perplexum* is the most similar species in shell outline and hinge features; the hinge dentition on the left valve is virtually indistinguishable from that of *I. frankfortensis*, the dentition of the right valve of *I. frankfortensis*, however, has thinner, more elongate, and more strongly fused posterior cardinals (3a and b). *Isorropodon bigoti* Cosel & Salas, 2001 has a similar shell outline but the hinge area is higher, and the teeth are more narrowly spaced and more strongly developed than in *I. frankfortensis*.

*Isorropodon curtum* Cosel & Salas, 2001 from off Mauritania is less elongate than *I. frankfortensis*, and *I. striatum* (Thiele & Jaekel, 1931) has internal striation and an exterior posterior ridge which are not visible on *I. frankfortensis*. This new species is not only the first certain record of *Isorropodon* from outside the Atlantic Ocean, but also the first fossil record of the genus. A fossil shell with similar external outline is *Callocardia* (*Agriopoma*) *californica* Clark, 1918, from the Oligocene San Lorenzo Formation of middle California (Clark, 1918). But with a length of 49 mm, that species reaches a much larger size than *I. frankfortensis*, and its hinge dentition is clearly veneroid rather than vesicomid (Clark, 1918, pl. 11, fig. 11).

**Distribution:** Cold-seep carbonates in the lower Miocene part of the Astoria Formation along the north shore of the Columbia River, Washington State, USA.

**Etymology:** After the vanished town of Frankfort near the type locality. Frankfort had a post office from 1890 until 1918; in 1947 the population had decreased to 11 residents, and in 1960 only two inhabitants remained.

#### Genus *Pliocardia* Woodring, 1925

*Pliocardia* Woodring, 1925:147.

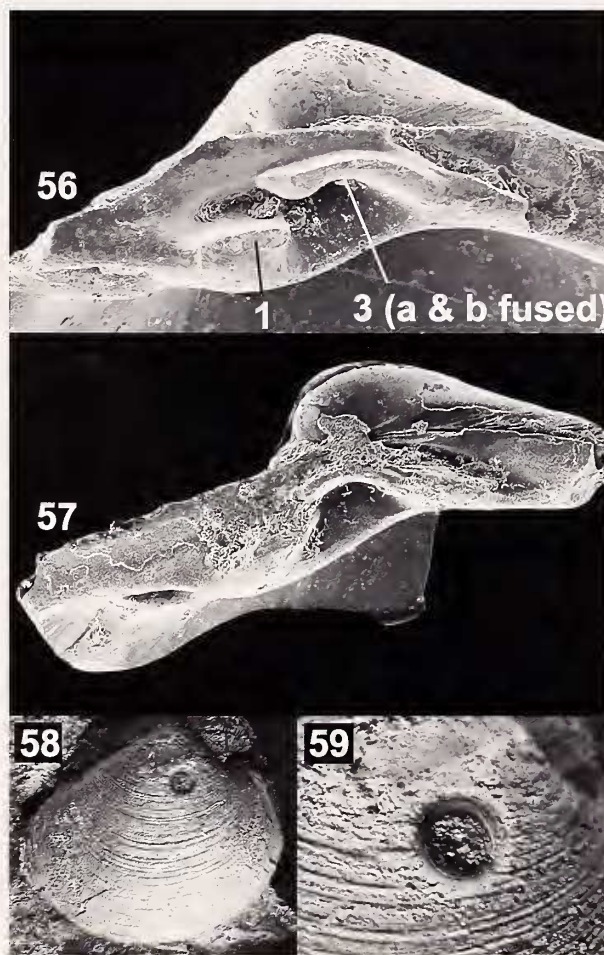
**Type species:** *Anomalocardia bowdeniana* Dall, 1903 (by original designation); Miocene, Jamaica.

**Remarks:** Woodring (1925) pointed out similarities between *Pliocardia* and *Vesicomya* regarding shell size, the lunule, and the similar arrangement of dentition. However, *Pliocardia* differs from *Vesicomya* by having thicker shells and a much thicker posterior cardinal tooth. The dentition of *Pliocardia* is, in fact, closer to that of *Archivesica* (see Figure 5). However, *Pliocardia* has a shorter anterior cardinal tooth in each valve, and lacks a subumbonal pit. Krylova & Janssen (2006) suggested that the Recent Japanese '*Vesicomya*' *crenulomarginata* Okutani, Kojima & Iwasaki, 2002 represents a living member of *Pliocardia*.

*Pliocardia*? sp.

(Figures 56–59)

**Description:** Shell oval in outline, with fine commarginal growth increments only; umbo subcentral, slightly prosogyrate. Hinge of right valve with elongate, moderately strong anterior cardinal (1) parallel to dorsal shell margin, positioned just anterior below beak; central cardinal (presumably fused 3a and b) moderately strong, convex; anterior end peg-like, thickened, positioned below beak; central part somewhat constricted; posterior part slightly thicker, paral-



Figures 56–59. *Pliocardia*? sp. from upper Oligocene seep deposits of the Lincoln Creek Formation, Washington State, USA. Figure 56. Right valve hinge. from the 'Canyon River site,' length 1.5 mm, USNM 534966. Figure 57. Another right valve hinge from the same locality, length 1.9 mm (USNM 534967). Figures 58–59. Specimen with a hole most likely drilled by a naticid from the Satsop River (LACMIP loc. 17747b), length 6.0 mm (USNM 534968).

lel to postero-dorsal shell margin. Deep groove between cardinal 3 and the thin nymph.

**Material and Distribution:** Four specimens from Oligocene seep carbonates in the Lincoln Creek Formation, Washington State, USA.

**Remarks:** The few available shells of *Pliocardia*? sp. from the 'Canyon River site' in Washington State are so fragile that complete shells could not be recovered; only hinges of the right valve are known. The dentition closely resembles that of the Miocene type species *Pliocardia bowdeniana* from Jamaica, thus we tentatively assign our specimens to this genus. A small specimen (7 mm long) with the same general outline as

Table 3

Range chart of vesicomyid genera treated herein. Dashed line indicates questionable occurrence.

Genus	Age	l. m. ~ l. Eocene	Oligocene	e.~m. Mio.	l. Miocene	Recent
<i>Archivesica</i>		—————	—————	—————	—————	—————
<i>Hubertschenckia</i>		—————	—————			
<i>Adulomya</i>		—————	—————	—————	—————	—————
<i>Calyptogena</i>					—————	—————
<i>Isorropodon</i>				—————	—————	—————
<i>Pliocardia</i>			-----	—————	—————	—————

*Pliocardia?* sp. but unknown hinge dentition from another Oligocene seep site in the Lincoln Creek Formation (LACMIP loc. 17747b, see Kiel, 2006 for details) has a parabolic hole with an inner diameter of 0.6 mm and an outer diameter of 0.9 mm. This hole was most likely drilled by a naticid. This is the first record of a chemosymbiotic bivalve in a cold seep with a drill hole in North America. Peckmann et al. (2002) reported naticids with drill holes from a seep site in the Lincoln Creek Formation but none of the bivalves from that site show drill holes (Peckmann et al., 2002; own observation). When Amano & Jenkins (2007) described drill holes in upper Eocene cold-seep bivalves from Hokkaido, they suspected that the Lincoln Creek Formation naticids could not cope with the presumed chemical deterrent in the soft tissue of these cold-seep bivalves (cf. Kicklighter et al., 2004), based on Peckmann's observation. However, considering the drilled *Pliocardia?* sp. reported here, it is necessary to reexamine this hypothesis.

#### REMARKS ON CRETACEOUS VESICOMYIDS IN JAPAN

Three vesicomyid species have been reported from Cretaceous strata (Albian to Campanian) of Japan, and these three species account for the apparent discrepancy between molecular age estimates and the geologic record of the family, as mentioned in the introduction (cf. Little & Vrijenhoek, 2003). Internal features like hinge dentition and pallial line of these species, however, have never been sufficiently examined.

When Kanie & Sakai (1997) illustrated small (= about 33 mm) elliptical specimens as *Calyptogena* (*Ectenagena*) sp. from the Albian Middle Yezo Group near Mikasa City, central Hokkaido, they did not describe the hinge structure and probably identified it only based on shell outline and surface sculpture. We

examined a fair number of newly collected specimens from this locality, all of which are present as internal molds (steinkerns), but none of them shows scars of their putative hinge dentition. As we have shown herein, such scars are often present in steinkerns of Cenozoic vesicomyids. Moreover, *Calyptogena* (*Ectenagena*) sp. at this site is associated with many solemyid specimens that are similar in size to *Calyptogena* (*Ectenagena*) sp. These solemyids show a considerable range of shell shapes and ornamentation, some of which resemble that of *Calyptogena* (*Ectenagena*) sp. as figured by Kanie & Sakai (1997). Thus we find it likely that this *Calyptogena* (*Ectenagena*) sp. is in fact a solemyid.

Hikida et al. (2003) illustrated a large bivalve from the 'Omagari seep site' of the Santonian to Campanian Upper Yezo Group near Nakagawa Town in northern Hokkaido as *Calyptogena* sp. They did not illustrate its hinge structure, thus its vesicomyid affinities can not be confirmed.

A large fossil bivalve (the holotype is 130 mm long) was described as *Vesicomya inflata* Kanie & Nishida, 2000, from the Cenomanian of the Middle Yezo Group in northwestern Hokkaido. The fossil locality consisted of two large carbonate concretions found as float in the river bed of the Sanjussen-zawa (Kanie et al., 2000). The available material at the Yokosuka City Museum consists of two articulated specimens (R. G. Jenkins, personal communication 2006), thus its hinge dentition could not be examined. Moreover, this species would be very large for *Vesicomya* (cf. Cosel & Salas, 2002), and has a deeply impressed asymmetrical lunule, a feature that can sometimes be seen in lucinids, but not in vesicomyids. In summary, the hinge dentition of all three of these Cretaceous vesicomyids proposed to date is unknown, and thus their vesicomyid affinities are uncertain.

Table 4

Fossil North Pacific vesicomids not discussed here because additional material was not available.

Species	Occurrence	Age	Status
<i>Adulomya</i> (?) <i>azarie</i> Shikama, 1969 [in Shikama & Masujima, 1969]	Japan	Pliocene	No hinge data
<i>Akebiconcha kawamurai elongata</i> Ozaki, 1958	Japan	Pliocene	Considered as <i>Archivesica</i>
<i>Calyptogena (Adulomya) uchimuraensis</i> <i>kurodai</i> Kanno & Tanaka, 1998 [in Kanno et al., 1998]	Japan	middle Miocene	Synonym of <i>Adulomya</i> <i>uchimuraensis</i> Kuroda, 1931
<i>Calyptogena akanudaensis</i> Tanaka, 1959	Japan	middle Miocene	No hinge data
<i>Calyptogena bosoensis</i> Kanie & Kuramochi, 2001	Japan	Pliocene	Hinge data insufficient
<i>Calyptogena</i> (?) <i>gibbera</i> Crickmay, 1929	California	early Pliocene to middle Pleistocene	Considered as <i>Archivesica</i> (herein)
<i>Calyptogena lasia</i> Woodring, 1938	California	early Pliocene to middle Pleistocene	Synonymized with <i>C. gibbera</i> by Squires (1991) but considered valid by Krylova & Janssen (2006)
<i>Calyptogena moraiensis</i> Suzuki, 1941	Japan	late Miocene	Synonymized with <i>C. pacifica</i> Dall, 1891 by Otatume (1942)
<i>Calyptogena nipponica</i> Oinomikado & Kanehara, 1938	Japan	late Miocene to Pliocene	Hinge data insufficient
<i>Calyptogena panamensis</i> Olsson, 1942	Costa Rica/ Panama	late Miocene or early Pliocene	Considered as <i>Calyptogena</i> by Krylova & Sahling (2006)
<i>Lamelliconcha kawadai</i> Aoki, 1954	Japan	early to middle Miocene	Similar to <i>Issoropodon</i> (outline) and <i>Waisiuconcha</i> (dentition)
<i>Solemya (Adulomya?) hachiyai</i> Nomura, 1935	Japan	late Miocene	No hinge data
<i>Vesicomya ellipsoidea</i> Kanie & Kuramochi, 2001	Japan	Pliocene	Hinge data insufficient

## DISCUSSION

With the exclusion of the doubtful Cretaceous vesicomids discussed above, the oldest confirmed vesicomid is *Archivesica* cf. *tschudi* from cold seeps in the late middle Eocene (Table 3). *Adulomya chinookensis* and *Hubertschenckia ezoensis* appeared more-or-less simultaneously in the late Eocene. During the Oligocene, a species potentially belonging to *Pliocardia* appeared in cold seeps in the northeastern Pacific Ocean along with *Isorropodon* in the early Miocene, with *I. frankfortensis* also at cold seeps. *Adulomya* started to colonize whale-falls in the Miocene, with *A. chitani* in the early Miocene (Amano et al., 2007) and the apparently whale-fall endemic species *A. hokkaidoensis* in the middle Miocene. These findings have several interesting implications. The proposed discrepancy between molecular age estimates [21.5–43.8 Ma according to Peek et al. (1997)] and first fossil occurrences of vesicomids [ca. 106 Ma according to Kanie & Sakai (1997)] as emphasized by Little & Vrijenhoek (2003) disappears with the removal of vesicomids from the Cretaceous record. The earliest vesicomids with confirmed vesicomid-type hinge architecture occur approximately between 36–38 Ma and are thus well within the range indicated by molecular estimates (Peek et al., 1997; Baco et al.,

1999). Considering that already three distinct genera were present at that time, the last common ancestor of the modern vesicomids lived earlier than that, but probably not much earlier.

The 'stepping stone' hypothesis predicted that vesicomid bivalves (among other taxa) underwent a significant radiation once whale falls were inhabitable for them (Baco et al., 1999; Smith & Baco, 2003). Kiel & Goedert (2006) showed that vesicomids did not occur at whale falls during the Eocene and Oligocene but only from the Miocene onward, and they suggested that the early whales had too little oil in their bones to sustain seep- or vent-like chemosynthetic ecosystems. However, they did not preclude the possibility that vesicomids underwent a major radiation once they started to adapt to whale-falls in the Miocene. But our new data does not seem to support this possibility either. The first radiation among vesicomids took place long before their first appearance at fossil whale falls, as indicated by the presence of three large-shelled vesicomid genera (e.g., *Adulomya*, *Archivesica*, and *Hubertschenckia*) at cold seeps in the Eocene and Oligocene. Although *Calyptogena* and *Isorropodon* first appear in the Miocene, these genera have not been found so far at Miocene whale falls. Four to five vesicomid species have been reported from modern whale falls (*Archivesica gigas*, *Adulomya elongata*,

*Calyptogena pacifica?*, and the *Archivesica soyoe-kilmeri* complex; cf. Naganuma et al., 2001 and Smith & Baco, 2003) which are from a broader range of genera than in the Miocene. Although we were not able to revise all known vesicomid species from the North Pacific (see Table 4), the presently available data shows little evidence for any correlation between the evolution of whales and of vesicomids, at least in this region. Admittedly, these suggestions are hampered by the scarcity of fossil whale falls, and even fossil cold seeps, in other parts of the world.

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Note added in proof: Dr. George Moore, after whom *Archivesica georgemoorei* is named, was unexpectedly killed in an auto accident on Oct. 4, 2007.

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